DESCRIPTION OF PLATE VII.

Fig. 1. *Heterolepidotus grandis*, Davis, one third nat. size.
Fig. 2. Scales, natural size.
Fig. 3. Anterior fin-ray of the pectoral fin, natural size.

On some Points in the Development of *Motella mustela*, L.

By George Brook, F.L.S.

[Read 6th November, 1884.]

(Plates VIII.–X.)

The eggs of *M. mustela* which I have been enabled to study were deposited in my aquarium during the months of May and June. They belong to the pelagic group of Teleostean eggs, and have usually one large oil-globule which keeps them floating on the surface of the water, although in a few cases I have found a cluster of from two to eight, or even more. These, however, were abnormal forms. Dr. Day, in his 'Fishes of Great Britain and Ireland,' i. p. 315, quotes from the 'Zoologist,' 1879, p. 476, the following words of Cornish:—"The nest wherein the spawn is deposited is invariably formed of the Common Coralline, *Corallina officinalis*, thrust into some cavity or crevice of a rock close to low-water mark." There must surely be some error in this observation, as it is manifestly entirely contrary to the nature of a pelagic egg to be retained in a nest. The eggs of all the other Gadidæ, so far as known, are pelagic, so that there is nothing exceptional in those of *Motella* being so.

The eggs are somewhat oval in shape, and are not all of equal size. The length of the longer axis varies from ·655 millim. to ·731 millim., and that of the shorter axis from ·640 millim. to ·716 millim. The shape, however, seems to vary considerably. Many are almost globular; and the oval shape seems often to be produced by three or four eggs touching one another. The slightest pressure alters the shape of the egg in this species, a feature which I have never observed in the egg of *Trachinus*. In normal eggs the single oil-globule is usually about ·11 millim. in diameter. In those eggs with more than one oil-globule there is usually about the same volume of oil as in the large single globule, but divided into larger or smaller globules, according to the number. A batch of eggs which were laid on the 28th of May had the majority of the eggs with more than one oil-globule, and curiously enough the eggs of this batch showed more irregularities in the early stages of development than any others that were observed. In any case eggs with a number of oil-globules either developed so irregularly as to die before hatching out, or the small oil-globules gradually coalesced to form one large one before the embryo left the shell. There was no exception to this rule, so that directly or indirectly an abnormal development of the oil-globules has its influence on the development of the embryo.

The earliest stage observed was that in which the disk is divided into sixteen cells. At this time the disk is oval in shape and measures about ·457 millim. by ·381 millim.; but these measurements are only approximate, as the form and size of the disk varies considerably in different eggs. Sometimes in this stage, at others not until the thirty-two cell stage, the disk becomes somewhat square in outline, and then measures ·441 millim. in diameter. The disk is then somewhat concave beneath, and its position is as usual a little eccentric. The disk then, with increasing cell-division, becomes more and more rounded in outline until about five hours after formation of sixteen-cell stage it has the appearance shown in section in fig. 1. Here the epidermal layer of the epiblast is well defined, and the surface of the disk lying on the yolk is perfectly flat.

It is about, or a little earlier than, this stage that the first collections of granules and nuclei are observed to form the *periblast* (Agassiz and Whitman *) =*parablast* of Klein †. In this respect the egg of *Motella* differs considerably from that of *Trachinus*. In the latter a minute collection of granules is to be found around the disk, even in the two-cell stage, that is to say on the completion of the first segmentation-process. These granules increase in size and number with each segmentation-process, until in the sixteen-cell stage they form quite a striking feature of the egg, as shown in plate 3. fig. 7 (Linn. Soc. Journ. Zool. vol. xviii.). In *Motella* no such gradual development occurs; and it is not until the segmenting disk presents the characteristic *morula* appearance that the first granules are observed. Again, in *Trachinus* the first row of cells forming the periblast is always uniform and complete before any cells of the second row are formed; whereas in *Motella* it is quite usual to find parts of a second and third row in their places before the first row is

* Proc. Amer. Acad. Arts and Sciences, xx. (1884).

† Quart. Journ. Micr. Sci. xvi. (1876).

completed. The nuclei in the periblast of *Motella* are also considerably larger in proportion to the size of the cell than is the case in *Trachinus*.

The exact nature of the so-called invagination-process to form the hypoblast was not observed, but an optical section taken when this process was well advanced would seem to confirm my views of the origin of the hypoblast in *Trachinus*. Figure 2 represents a surface view of this stage, and fig. 2 *a* the same as seen in section. My opinion at present is that the cells of the periblast are pushed under the germinal disk until they cover the whole floor of the segmentation-cavity, and that cells absorbed from this layer and free cells from the yolk contribute to a very great extent to build up the invaginated layer, if indeed it is not at first formed entirely from these sources. I have discussed this question more fully in a paper on the "Origin of the Hypoblast" (Quart. Journ. of Micros. Sci. Jan. 1885, p. 29), and it will be useless to renew the discussion here. The cells of the new layer in *Motella* are, however, so much larger than is usual in Teleostean ova that their exact position is easily made out; and to my mind it seems impossible to maintain that cells so large and well-defined in outline could be formed by an involution and budding of the tiny cells of the germinal disk, which, under a magnifying power of 100 diameters, are scarcely distinguishable.

The cells in the segregated hypoblast in fig. 2 are very distinct and quite sharply defined in outline, while with the same magnifying power in *Trachinus* these cells are indistinguishable. The embryonic shield at this stage is also larger in proportion to the size of the egg than that of *Trachinus*; and when the embryo begins to make its appearance, this shield occupies the greater portion of a surface view of the egg. Before the keel can be made out, the cells in the centre of the shield become smaller and smaller, until, as shown in fig. 3, they can scarcely be made out with an amplification of 50 diameters. It is quite evident at a very early stage that the young *Motella* embryo will be very long and narrow, and before the appearance of Kupffer's vesicle it occupies half the circumference of the egg. I have nothing new to report in the early development of the embryo, but it will be interesting to compare the times at which the different organs appear with those of *Trachinus*. For instance, Kupffer's vesicle, which in *Trachinus* appears before any protovertebræ are formed, and long before the closure of the blastopore, does not make its appearance in *Motella* until at or after the closure of the blastopore, and at a time when there are at least six or eight protovertebræ. The vesicle itself is also differently constituted. In *Trachinus* it consists of a large single amber-tinted body, which is quite transparent and shows no cell-structure with a magnifying power of 100 diameters; whereas in *Motella* it consists of a solid mass of rounded cells which increases in size with the formation of the intestine, and gradually disappears again as the latter is pushed backwards towards the tail. In *Trachinus* Kupffer's vesicle disappears before the tail begins to grow free from the yolk, and also before the heart begins to pulsate; while in *Motella* the tail has grown free some distance and got a curious twist in it (fig. 6) before the vesicle disappears. In *Motella* also the tail grows as a free prolongation for some time before the heart begins to pulsate. The first formation of the heart and alimentary tract takes place in *Trachinus* at the time of the closure of the blastopore, and when Kupffer's vesicle is increasing in size. In *Motella* they do not arise until the blastopore has been closed some time, and Kupffer's vesicle has passed its maximum development. Early on the third day the embryo presents the appearance shown in fig. 5. The part of the yolk immediately under the head then contracts, and during the next twenty-four hours the boundary of the existing cavity is pushed back so as to enclose the space in which the heart is formed, as shown in fig. 6. Early on the fourth day it was noticed that the oil-globule in all eggs had an investing membrane binding it to the yolk. This probably consists of hypoblast, and was left behind with the advance of the blastodermic rim over the yolk, as suggested by Ryder. On the fifth day the membrane investing the oil-globule contains from two to five pigment-spots.

The embryos hatch out from 5½ to 6 days after fertilization under the following conditions of temperature. The temperature of the water in the tanks varied during the six days from 55°·5 F. to 51°·3, but during the daytime the temperature of the water in which the eggs were developing would usually rise to 60°, or even 62°, and then gradually sink again during the night to that of the water in the tanks. A ventral view of the newly-hatched fish is shown in fig. 7, and a side view in fig. 7 *a*; soon after hatching, however, the continuous embryonic fin expands dorsally and ventrally, as shown by the dotted lines in fig. 7 *a*. A comparison of these figures with those of the newly-hatched embryo of *Trachinus* (Linn. Soc. Journ. Zool. vol. xviii. pl. 6. figs. 27 and 28), shows at once that the *Motella* embryo is not so advanced in development as that of *Trachinus*. This of course might be expected from the earlier period at which it hatches. The head is strangely backward in development in the newly-hatched fish, and, as we shall see, presents very curious features during its later modifications. The thickening for the ventral fins is only just visible, as will be seen in fig. 7. It is about this time that the air-bladder is budded off from the respiratory section of the alimentary tract just in front of the liver. It does not, however, become very distinct until the body becomes more thickly pigmented, when it is easily seen as a clear space surrounded by pigment. The embryo in this stage measures 2·25 millim. long by ·55 millim. deep. At the time of hatching there is little pigment on the body, but this is quickly deposited, until when two days old there is so much pigment about the jaws and mesenteron as to make further development difficult to follow. Figures 8 and 8*a* give ventral and lateral views of the embryo, about forty hours later than fig. 7. The yolk-sac has been considerably absorbed, leaving the heart in a large pericardiac cavity, the remains of the segmentation-cavity, which persists so long as any yolk is left. The ventral fins have grown considerably, and are now nearly as large as the pectoral. The principal changes, however, are in the head. The brain-lobes have increased very considerably in size, are well marked out for the first time on a lateral view, the cerebellum has now been segmented off, and the medulla oblongata is very much increased in bulk. Changes now take place in the head which are difficult to follow; and further work on this point is necessary in order to understand them properly. The dorsal portion of the head grows much more rapidly than the ventral portion up to a certain point. The result is that a cranial flexure is produced which is different from anything I have observed in other Teleosteans, and is in some respects comparable with the early embryonic condition of Elasmobranchs. In the latter, it is true that the characteristic feature of this flexure is that the mid brain is pushed forward until it forms the most prominent part of the body, and is in fact, for the time being, the termination of the body-axis. In Elasmobranchs, however, the mouth is situated ventrally in the adult, so that the embryonic mouth and brain have not again to change their relative position, as would be the case in a Teleostean with an embryonic cranial flexure. In *Motella* the mid brain can scarcely be said to be *anterior* to the fore brain; but, as will be seen from figures 9 and 10, it occupies a position quite as prominent. The truth is, that the brain develops very rapidly, while the jaws remain comparatively undeveloped, so that the fore brain is pushed forwards and downwards until the mid brain lies completely over it. Another consequence of this rapid growth is that the mouth takes up a temporary ventral position (figs. 9 & 10). At this time the mouth is only slightly open, and the lower jaw is not so prominent as the upper one. Their relative position will easily be understood by reference to fig. 9 *a*. When, however, the brain has reached its maximum development, the ventral portion of the head begins to play its part, and the cranial axis is gradually pushed back into its normal position as the lower jaw increases in size. This time the greatest development is on the extreme ventral surface, and the lower jaw now outstrips the upper one in dimensions. The time occupied by all these changes is from 6 to 6½ days, and their course will easily be followed by a comparison of figs. 7 to 14.

About a day after hatching, a small clear vesicle arises in the immediate vicinity of the liver, which is probably the gall-bladder. This vesicle remained transparent as long as the young fish lived. In *Cyclopterus lumpus*, however, I have observed a similar gland, which gradually becomes filled with a bright green fluid, seen at a glance in the living embryo. As is usual with pelagic fish-eggs, there is no circulation either embryonic or vitelline in *Motella* before hatching, nor, indeed, for some days afterwards. From six to seven days after hatching a rudimentary circulation was observed, but it was very faint, and no vessels were properly formed. Soon afterwards the young fish died, so that I have no reliable data on this point. The arrangement of the vessels in the early circulation of Teleostean embryos seems to vary very much in different forms that have been studied; and so far as I am aware no thorough comparative study of this development has yet been made. In *Cyclopterus* I have found an arrangement differing in many important points from other forms already described, and *Motella* seems to have something in common with *Cyclopterus*. There is, first of all, an aortic circulation pushed backwards as far as the anus, and the corpuscles return in a lower area of the same tissue before the vessels themselves are formed. From this system a branch is given off near the constriction in the intestine, which soon bifurcates, sending a branch backwards to the anal gut, and a branch forwards to the heart. It is this lower return branch to the heart which would seem to be the homologue of the large vessel in *Cyclopterus*, which distributes the blood around the yolk before it is again collected in the heart. In *Motella*, also, this vessel passes over what is left of the yolk on its way to the heart. Further work, however, is needed on this point before any true analogy can be established.

During the first few days of the embryo's free existence, the pectoral fins far outstrip the ventrals in dimensions. A reference to fig. 11 shows the pectorals as large, flat, leaf-like expansions, while the ventrals are thick and short, with an undulating margin, and are deeply pigmented.

Agassiz (" On the young stages of some Osseous Fishes," part iii., Proc. Amer. Acad. of Arts and Sciences, new series, vol. ix. 1882) expresses a doubt whether the young stages which he has figured as *Motella argentea* belong to that genus, and are not rather the young of *Onus*, in which the ventrals are developed to an extraordinary degree in the young, reminding one of the specialized development in Flying-Fishes. I am not aware whether Agassiz's figures have since been identified; but if they really represent *Motella*, it is easy to see how the ventral fin, as represented in my fig. 11, could be developed so as to agree with Agassiz's pl. vii. fig. 1.

There appears to be one point in which the Gadidæ differ in their development from all other Teleosteans of which the development is known, and that is the late period at which the anus opens externally on the ventral surface. The exact time at which this takes place is not known. Ryder figures the young of the Cod 7 days after hatching (" Contrib. to the Embryog. of Osseous Fishes:" Report of the Commissioner of Fish and Fisheries for 1882. Washington, 1884, pl. xii.), with the intestine and anal gut having no opening externally; and in the oldest embryos I have had of *Motella* (*i. e.* 6½–7 days after hatching) I have found the same to be the case. It would appear, then, as if the young Gadidæ were not in a position to take solid food at nearly so early a period in their development as is usually the case with Teleostean embryos.

There is another point which is worthy of notice in the development of pelagic ova, namely the length of time which the embryo spends *within* the egg. The following is a list of the principal species of pelagic eggs observed, where the observers state the time of hatching:—

Julis vulgaris (Hoffmann): 52 hours.

Scorpæna porcus (Hoffmann): 58 hours.

Scorpæna scrofula (Hoffmann): 58 hours.

Fierasfer acus (Hoffmann): probably 58–60 hours.

Spanish Mackerel (Ryder): 24 hours, some even 20 hours; and, if temperature unusually low, 36 hours.

Codfish (Ryder): 20 days (38° F.); has been known to hatch in 13 days (45° F.).

Codfish (Sars): 16 days; 18 days at very low temperature.

Cunner (*Ctenolabrus cæruleus*) (Kingsley and Conn): 2 days.

Fierasfer acus (Emery): 3rd day.

Cunner and others (Agassiz and Whitman): 50 hours.

Pseudorhombus oblongus (Agassiz and Whitman): 40 hours.

Trachinus vipera (Brook): 10th day, 58° F.

Motella mustela (Brook): 6th day, 55°–60° F.

It will be noticed that the embryos in the above list hatch out at a time varying from 20 hours to 20 days. The question is, how far this disparity is a natural feature of the egg, and how far it depends on temperature. I have already called attention to the varying period at which the embryos of *Trachinus* hatch out according to the temperature; and there is no doubt that within certain bounds a higher or lower temperature will proportionately accelerate or retard the development of this species. Unfortunately we have no details of the temperature at which most of the observations were made. The species mentioned by Hoffmann * were studied at Naples in the spring and summer, when the temperature of the surface of the sea would be very high, and thus far the short time taken to hatch out may *in part* be accounted for. Ryder's observations † on the Spanish Mackerel would also be carried on at a high temperature, but even taking that into consideration, the development is remarkably rapid. The same may be said of the observations of Kingsley and Conn ‡, and Agassiz and Whitman §. The Codfish spawns in the winter time; and we notice at once the much greater time spent by the embryo within the egg, and also that to some extent the date of hatching depends on the temperature. In some of the non-pelagic eggs laid in the winter, such as the Trout and Salmon, a

* Natuurk. Verh. d. koninkl. Ak. Amsterdam, xxi. (1881).

† Bull. U. S. Fish. Comm. i. (1881).

‡ Mem. Bost. Soc. Nat. Hist. iii. (1883).

§ Proc. Amer. Acad. of Arts and Sciences, xx. (1884).

sudden rise of temperature will often kill the eggs; and it is a fact well known to pisciculturists that a greater percentage of the ova of these forms is hatched out successfully when the temperature is kept low.

How far, then, a summer-breeding fish requires a high temperature and a winter-breeding fish a low one depends doubtless on features which have been adopted owing to the influence of the environment. There is still, however, a certain range of temperature to which each developing embryo can accommodate itself according to its kind; and I cannot help thinking that until we know more of the influence of this varying range, we shall not be able to compare satisfactorily the development of one fish with another.

DESCRIPTION OF THE PLATES.

Lettering used throughout the Plates.

a. = archiblast.
a. s. = auditory sacs.
b. = clear glandular body (probably the gall-bladder), referred to in text, p. 303.
b. c. = breathing-chamber.
br. = branchial arches.
c. = cerebellum.
cc. = loose cells and nuclei lying on the floor of the segmentation-cavity.
c. f. = caudal portion of the continuous embryonal fin.
e. s. = embryonal shield.
f. b. = fore brain.
h. = heart.
hy. = hypoblast (true) or secondary entoderm.
h. b. = hind brain.
K. v. = Kupffer's vesicle.
l. = liver.
l. j. = lower jaw.
m. = mouth.
msb. = mesoblast or mesoderm.
m. b. = mid brain.
mn. = mesenteron.
m. o. = medulla oblongata.
n. = notocord.
n. p. = nasal pit.
o. g. = oil-globule.
opt. = optic lobes.
p. = periblast (parablast) or nuclear zone.
p. s. = pericardial sinus.
p. e. = primary entoderm or hypoblast.
p. f. = pectoral fin.
p. s. = pigment-spots.
p. v. = protovertebræ.
py. = pyloric constriction of the intestine.
s. b. = swim-bladder.
s. c. = segmentation-cavity (both before and after its extension around the yolk).
u. v. = urinary vesicle.
u. j. = upper jaw.
v. f. = ventral fin.
y. = yolk.
z. r. = zona radiata.

The forming cartilages of the jaws are shown as dotted tissue in figs. 9, 9 *a*, 10, & 11.

The details of the alimentary tract are more hidden by pigment than is shown in figs. 10 & 11.

The direction of the circulation is indicated by arrow-heads in fig. 13.

Plate VIII.

Fig. 1. Optical section of the whole egg on the first day, showing segmentation-mass, with the epidermic layer of the epiblast already differentiated, and the periblast around the rim of the disk.

2. Surface view of egg (as floating) just over one day old, showing cell-formation in the embryonal shield.

2 *a*. Optical section of same stage, showing formation of the hypoblast and free cells in the yolk and on the floor of the segmentation-cavity.

3. View of the embryonal shield 6 hours later than fig. 2, showing first formation of the embryo.

3 *a*. Optical section of fig. 3, showing the notochord.

4. Surface view of the embryo 5 hours later than fig. 3.

5. Surface view of embryo about 12 hours later than fig. 4 (early on third day).

5 *a*. Caudal end of embryo in fig. 5, enlarged to show the caudal plate (Ryder), and the structure of Kupffer's vesicle.

6. View of embryo as floating early on 4th day, and 24 hours later than fig. 5.

Plate IX.

Fig. 7. Ventral view of newly hatched embryo.

7 *a*. Side view of same embryo. Dotted line shows the extension of the embryonal fin some hours after hatching.

8. Ventral view of young fish 1½ day old.

8 *a*. Side view of same stage.

9. Head of young fish 2 days after hatching, showing the cranial flexure and the ventral position of the mouth.

9 *a*. Ventral view of the head in same stage, showing the mouth and the arrangement of the bony plates.

Plate X.

Fig. 10. Anterior portion of a young fish 2½ days old, showing arrangement of pigment and the further development of the cranial flexure.

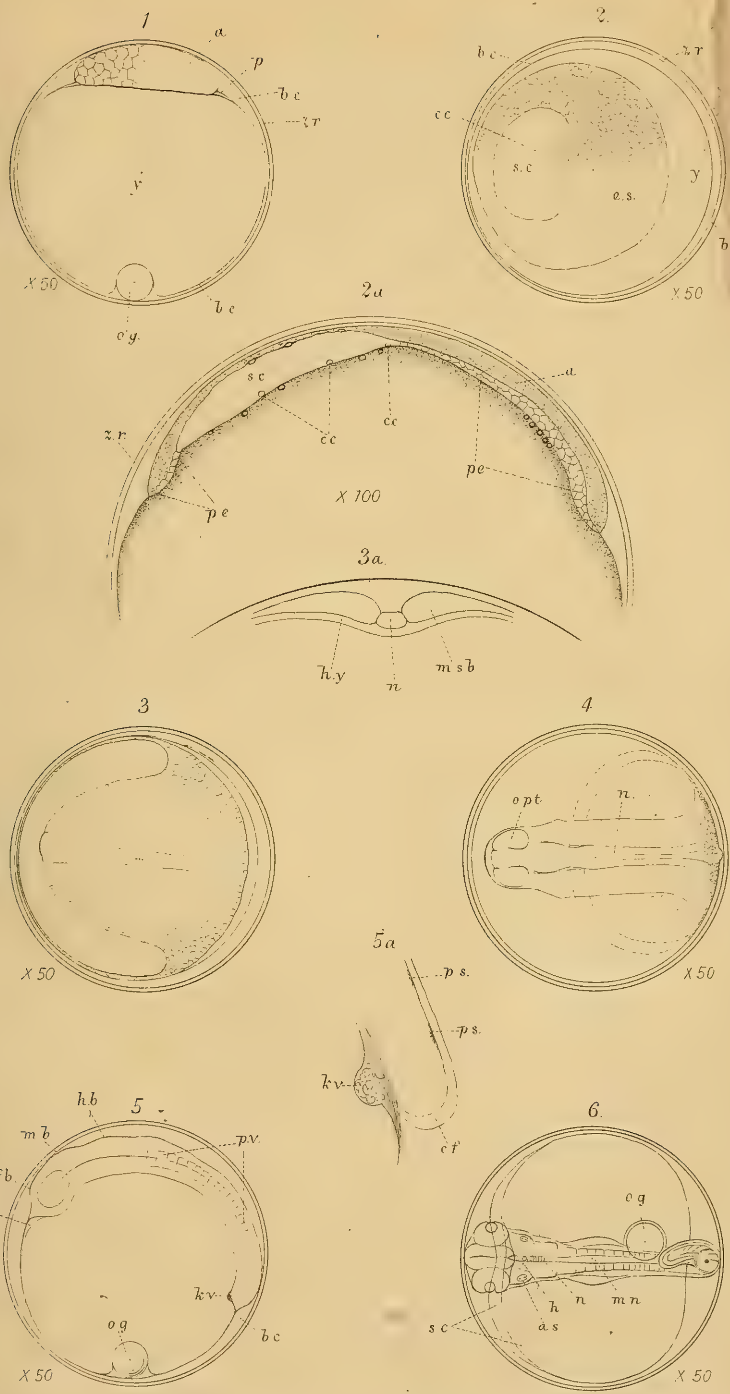
10 *a*. Dorsal view of same stage.

11. Anterior end of a young fish 4½ days old, showing further development of the jaws.

12. Anterior end of a young fish 5½ days old, showing the change in the relative position of the brain brought about by the rapid development of the jaws.

13. Portion of young fish 6½ days old, showing rudiments of circulation.

14. Dorsal view of anterior portion of young fish in same stage.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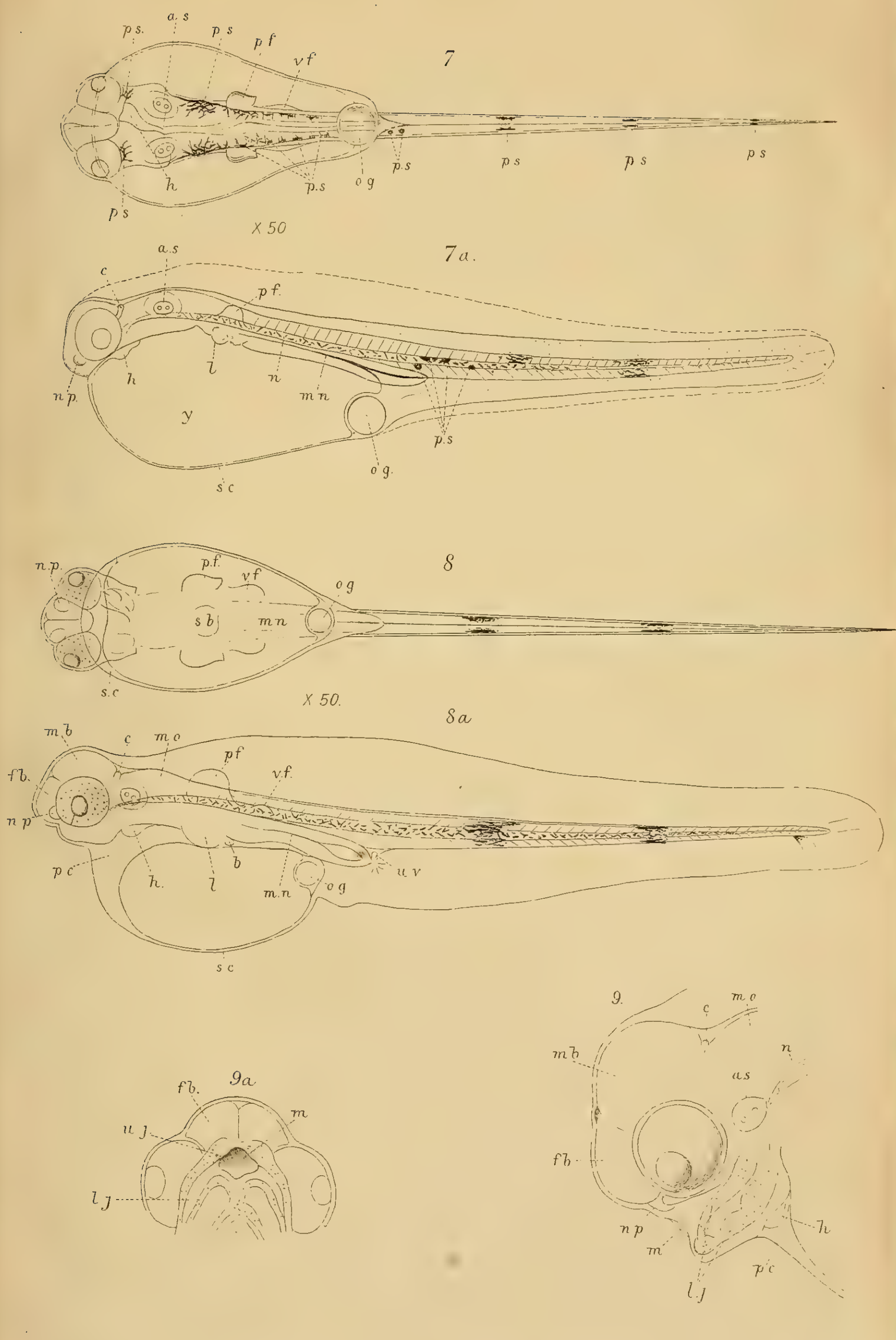

E. Carter sc. DEVELOPMENT OF MOTELLA MUSTELA. Mintern Bros imp.

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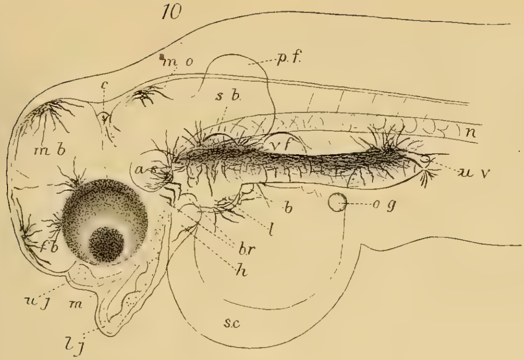

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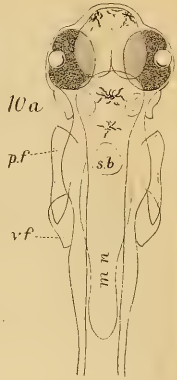

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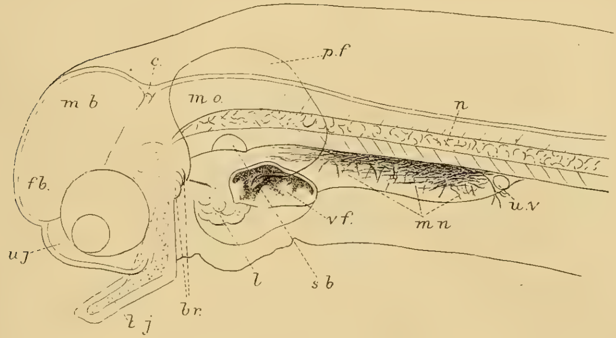

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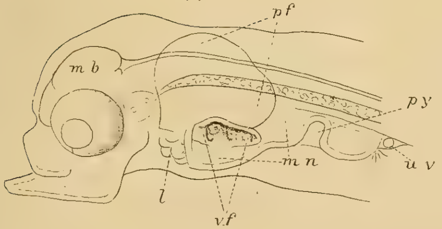

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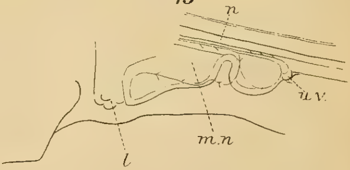

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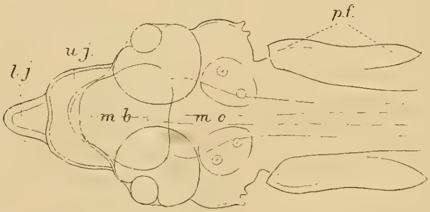

DEVELOPMENT OF MOTELLA MUSTELA.

Mintern Bros: imp.